

The Invasive Ant Fauna (Hymenoptera, Formicidae) of Laysan Island, Hawaiian Islands National Wildlife Refuge

G. T. W. McClelland^{1,2} and I. L. Jones²

¹Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa; email: mgreg@sun.ac.za

²Department of Biology, Memorial University of Newfoundland, St. John's, NL, Canada A1C 3X9

Abstract. Ants are not native to any of the Hawaiian Islands and invasive ant impacts on Hawaiian ecosystems have been profound, so documentation of ant diversity is crucial to understanding and managing these alien species. Changes to the invasive ant fauna on Laysan Island, Northwest Hawaiian Islands, were documented in 2005, fifteen years after the previous (1990) survey of the island. Six species were found on the island, all previously recorded. The common tramp ant *Monomorium pharaonis* was found to have greatly expanded its range to become the dominant ant on Laysan. During the same period, the range of the previously dominant ant species, *Tetramorium bicarinatum*, greatly decreased and the species was limited to the dense vegetation areas around the island's central lake. *Tetramorium simillimum*, possibly the most recent introduction to the island, and previously the second most widespread species, was not located in surveys and is possibly extirpated. An invasive ant species has apparently not become established on Laysan in almost 20 years suggesting current quarantine measures are a successful deterrent to colonization events.

Key words: invasive ants, Laysan Island, *Monomorium pharaonis*, *Tetramorium bicarinatum*

Introduction

Ants are common and often destructive invaders of ecosystems (Lubin 1984). They have the potential to negatively affect both invertebrate and vertebrate species through predation and resource competition (Le Breton 2005, Philpott et al. 2005, Gerlach 2004). In addition, invasive ants may negatively affect plant species by forming mutualistic relationships with homopterous insects that spread disease or disrupting mutualistic relationships between endemic plant species and arthropods (Lach 2007, Ness and Bronstein 2004, Bach 1991). These effects can be especially devastating on oceanic islands such as Hawaii where the native fauna has evolved in the absence of ants and lacks competitive or antipredation adaptations (Paulay 1994). It is of great value to monitor the species composition and distribution of introduced ants on oceanic islands, not only as a benchmark for the global spread of introduced species, but because the species composition may shift over time (Wilson and Taylor 1967). These shifts often occur because of new introductions that change the distribution and abundance of previous invaders (Haskins and Haskins 1965). Examining such interactions may lead to better understanding the mechanisms of their success and subsequently lead to improved management and prevention of future introductions (Tsutsui and Suarez 2003). This study reports changes to the introduced ant fauna on Laysan Island, Northwest Hawaiian Islands twenty years after the introduction of the common tramp ant *Monomorium pharaonis* (L.)

With the exception of Midway Atoll, Laysan has the highest number of invasive ant species historically documented in the Northwest Hawaiian Islands (Nishida 2001). The

spread and transportation of invasive ants was a common occurrence when Laysan first began receiving visitation by Europeans in the mid-nineteenth century (Illingsworth 1917). Laysan's history as a guano-mining island and the ship traffic associated with it, as well as occasional visits from feather poachers, lead to the frequent introduction of invasive ants, so that four species were present by the first arthropod survey of the island in 1896 (Emery 1899). Further visitations by military personnel and scientific researchers increased the number to eight by 1962. Though this number has been cited as higher (Butler and Usinger 1963), Fullaway (1914) mistakenly identified *Monomorium destructor* (Jerdon) as *Monomorium gracillimum* (F. Smith) (Conant and Rowland unpublished) and it is likely Butler (1961) mistakenly reported *Monomorium minimum* (Buckley) instead of *Monomorium liliuokalani* (Forel) in his review of the island's arthropod fauna. In addition, *Camponotus variegatus* (F. Smith) should not be included because it was collected on board a ship in close proximity to Laysan, not the island itself (Butler and Usinger 1963). The last two ant introductions were thought to have occurred in the early 1980's. *Monomorium pharaonis* was introduced circa 1984 (Conant and Rowland unpublished). The year of introduction of *Tetramorium similimum* (Mayr) is not known but sometime between 1984 and 1990 is likely (Conant and Rowland unpublished). A thorough census of the island's ant fauna had not occurred since 1990 (Conant and Rowland unpublished), leaving the current invasive ant community and their distributions poorly known.

In summary, the objective of the present study was to document the current (2005) ant species diversity and distribution of Laysan Island and compare it to the known ant community.

Materials and Methods

Study area. Observations were conducted at Laysan Island (25° 46' N, 171° 03' W) in the Hawaiian Islands National Wildlife Refuge. Located 1495 km northwest of Honolulu, Laysan is an extremely remote 397 ha coral sand island featuring a 70 ha hypersaline lake in the center. Once left completely void of vegetation by introduced European rabbits (*Oryctolagus cuniculus*) (see Ely and Clapp 1973), Laysan Island is currently in the midst of an island restoration project undertaken by the U.S. Fish and Wildlife Service. In 2004, approximately 217 ha, or 66% of available area, was vegetated (McClelland unpublished). The dominant vegetation is bunchgrass (*Eragrostis variabilis*), but includes dense mixed-vegetation communities (*Scaevola taccada*, *Ipomea pes-capae*, *Sicyos pachycarpus*) bordering much of the lake. Several stands of the non-native beach heliotrope (*Tournafortia argentea*) and Indian fleabane (*Pluchea indica*) are also present (see Lamoureux 1963 and Newman 1988 for more detailed vegetative community descriptions).

Laysan is the site of a year-round U.S. Fish and Wildlife Service research station and receives several visitations by ship per year. Since the establishment of the station in 1991, strict quarantine measures including the import of only new or recently frozen clothing and gear have been in place. More rigorous measures including a ban on fresh food and hull inspections for primary vessels and small boats were incorporated in 2005, following the present study (C. Rehkemper personal communication).

Bait card surveys. Wedge-tailed Shearwater (*Puffinus pacificus*) and Bonin Petrel (*Pterodroma hypoleuca*) burrows extensively undermine much of Laysan Island and travel through nesting areas poses a high risk of disturbance (Moulton and Weller 1984). Therefore the island was surveyed for ants in the early winter during a brief period when shearwater chicks had fledged and petrels had yet to start occupying burrows. A total of 182 sample locations in the island's interior were established in a 100 m grid pattern. An additional 66 locations around both the inner and outer perimeters of the vegetation were added to the survey, for a total of 248 locations (Figure 1). Each location was surveyed once between

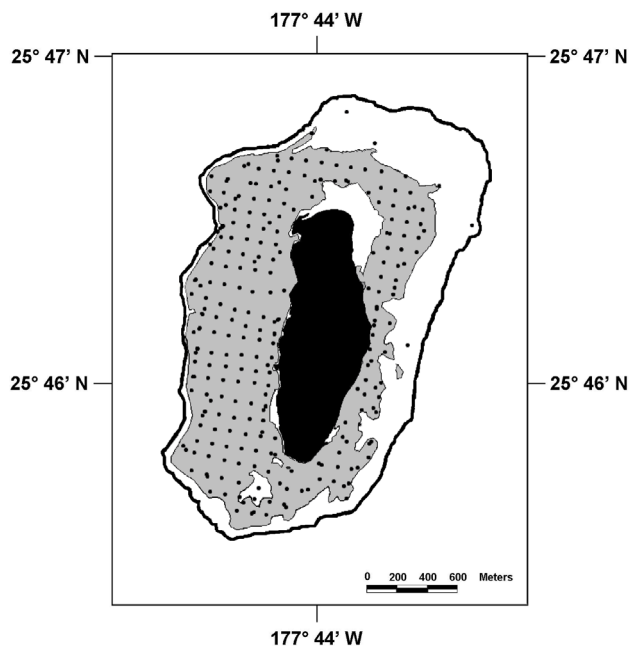


Figure 1. Bait card sampling locations on Laysan Island, Northwest Hawaiian Islands. Grey indicates vegetated areas; black is the hypersaline lake at average winter level.

January 4th and 10th, 2005.

For every survey location a 1cm³ cube of Spam[®] (ham, pork, sugar, salt, and water) and 1 ml each of peanut butter and honey were placed on a 4x6-inch index card. Each card was placed under a wire cage to prevent interference from shorebirds and Laysan Finches (*Telespiza catans*). The cards were left for 2–3 hours before being collected and immediately transferred to a sealed plastic bag. Because occupation of baits may be more reflective of competitive ability rather than abundance (Way et al. 1998), a brief (<2 min) ground search of the immediate area was also conducted at each survey location.

Vegetation associations. At each bait card survey location, the 3 most abundant plant species within a 10 m radius were recorded in order of rank. Using these data, locations were later sorted into 5 vegetation types: bunchgrass, dense mixed-vegetation, bunchgrass/dense vegetation, beach heliotrope, and lake edge (*Cyperus laevigatus*/*Sesuvium portulacastrum*).

Pitfall traps. Ant species were sampled using pitfall traps at the southern end of the lake. Traps were spaced approximately every 12 m and consisted of a 266 ml plastic cup placed in a PVC tube and filled with approximately 100 ml of soapy water. Pitfall traps were active for 48 hours every 4 weeks. Sixty-eight traps were active from November 2003 to May 2004, but declined to 34 from December 2004 to March 2005.

Statistical analysis. Correlations between ant species presence and vegetation type were tested using a binomial logistic regression model with a logit link function (Hosmer and Lemeshow 1989) in Minitab version 13 (Minitab Inc. 2000). All results were considered significant when $p \leq 0.05$.

Table 1. Invasive ants recorded on Laysan Island, Northwest Hawaiian Islands, as of 2005.

Scientific Name	Past Scientific Names*	First Reported	Last Reported	Current Status
<i>Cardiocondyla minutior</i> (Forel, 1899)	<i>C. nuda</i>	1959 ³	This study	Present
<i>Hypoponera punctatissima</i> (Roger, 1859)	<i>Ponera punctatissima</i> , <i>P. kalakauae</i> , <i>P. gleadowi</i>	1896 ¹	This study	Present
<i>Monomorium destructor</i> (Jerdon, 1851)	<i>M. gracillimum</i>	1896 ¹	1923 ³	Extirpated
<i>Monomorium floricola</i> (Jerdon, 1851)	N/A	1959 ³	This study	Present
<i>Monomorium liliuokalanii</i> (Forel, 1899)	<i>M. minutum</i> <i>M. monomorium</i>	1912 ²	1912 ²	Extirpated
<i>Monomorium pharaonis</i> (Linnaeus, 1758)	N/A	1984 ⁵	This study	Present
<i>Pheidole megacephala</i> (Fabricius, 1793)	N/A	1959 ⁴	1959	Extirpated
<i>Plagiolepis alluaudi</i> (Emery, 1894)	N/A	1959 ³	This study	Present
<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	N/A	1896 ¹	1912 ²	Extirpated
<i>Tetramorium bicarinatum</i> (Nylander, 1846)	<i>T. guineense</i>	1896 ¹	This study	Present
<i>Tetramorium simillimum</i> (Forel, 1899)	N/A	1990 ⁵	1990 ⁵	Not recorded, possibly extirpated

*refers only to past surveys of the Northwest Hawaiian Islands
¹Emery 1899, ²Fullaway 1914, ³Bryan et al. 1926, ⁴Butler and Usinger 1963, ⁵Conant and Rowland unpublished (1990).

Results

Ant species present. A total of six ant species were collected, all previously recorded on the island (Table 1). Ants were collected on 93% of bait cards placed in vegetated areas ($n = 242$). The only vegetation type in which ants were consistently absent was the lake edge association. Ants were rare in unvegetated areas and absent from outer beach areas despite high amounts of marine debris including washed-up logs. Vegetation appeared to be required for colony establishment in most locations of Laysan due to the sandy soils. Ants nested in and around the root system of plants, hollow portions of plants, or under dense vegetative cover. The highest densities of ants were consistently found under beach heliotrope, likely due to greater soil stability and the benefits associated with the high amounts of leaf litter such as increased cover and foraging opportunities.

Only 13% of locations with ants yielded more than one species ($n = 227$). The dominant ant in each location monopolized bait cards and on only 3 bait cards did the second species comprise more than 5% of collected individual ants. Ant species abundance by individuals collected and number of collection sites is presented in Figure 2.

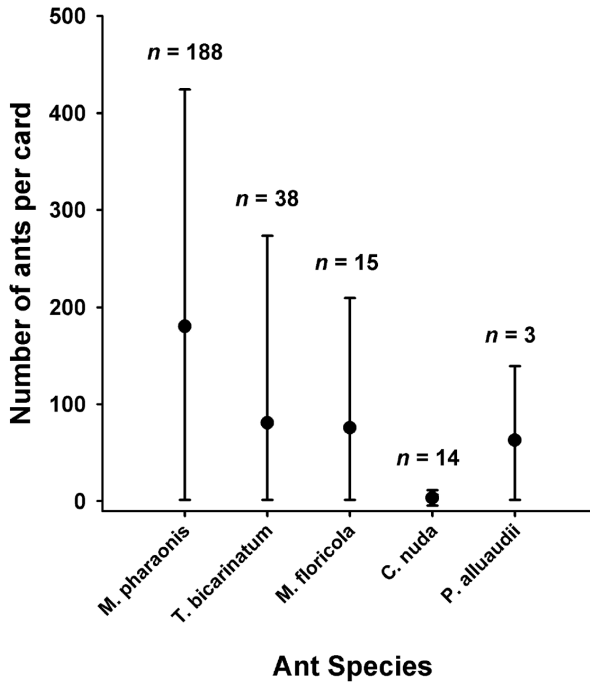


Figure 2. Mean (\pm standard deviation) ant captures per bait card on Laysan Island, North-west Hawaiian Islands.

Monomorium pharaonis. *Monomorium pharaonis* was by far the most common ant on the island (Figure 3). It was found in all habitat types and dominated the bunchgrass areas where it was in most instances the only species recorded. Most bunchgrass clumps housed a nest. *Monomorium pharaonis* was also extremely common in the camp area where barriers were required to keep them out of most food items, electrical equipment, and bedding. The presence of *M. pharaonis* was strongly correlated with bunchgrass habitat ($G = 12.298, p \leq 0.001, n = 248$), but the species could also be found on the periphery of mixed-vegetation areas.

Tetramorium bicarinatum. The presence of *T. bicarinatum* was strongly correlated with the dense mixed-vegetation habitat type ($G = 27.294, p \leq 0.001, n = 248$) (Figure 4). Though small numbers of *T. bicarinatum* could be found foraging in bunchgrass areas, this was usually when in close proximity to mixed-vegetation and the species rarely based its colonies there.

Monomorium floricola. *Monomorium floricola* was found in both *M. pharaonis* and *T. bicarinatum* dominated areas. Though species presence could not be predicted by habitat type based on the vegetation classifications of this study, they did not occur in open bunchgrass areas and appeared to strongly prefer areas with some vegetative cover such as *S. taccada* where they were locally abundant (Figure 5).

Cardiocondyla minutor. *Cardiocondyla minutor* was the only species collected by bait cards that was never the dominant species on the card. Instead, the species was more often

located with ground searches and may have been more widespread than indicated (Figure 6). Collections of *C. minutior* were most common in transition areas between bunchgrass and the thicker vegetation around the lake.

***Plagiolepis alluaudi*.** *Plagiolepis alluaudi* may have had a very limited distribution on Laysan, only being recorded in 3 isolated locations in bunchgrass habitat with an additional single specimen found dead in the USFWS camp (Figure 7). Locally abundant, nests were noticeably larger than those of *M. pharaonis* and found in bunchgrass clumps. *Plagiolepis alluaudi* appears to have the ability to survive in areas dominated by aggressive ant species, and foraging distance may be limited (Smith 1958). Therefore, more intensive surveys for this species may have yielded more locations.

***Hypoponera punctatissima*.** *Hypoponera punctatissima* has been described as most often locally rare with elusive habits (Delabie and Blard 2002), a trend it followed on Laysan as it was not recorded with bait cards or ground searches. Instead, all collections of this species totaled six alates from pitfall traps. Surveys failed to locate a nest.

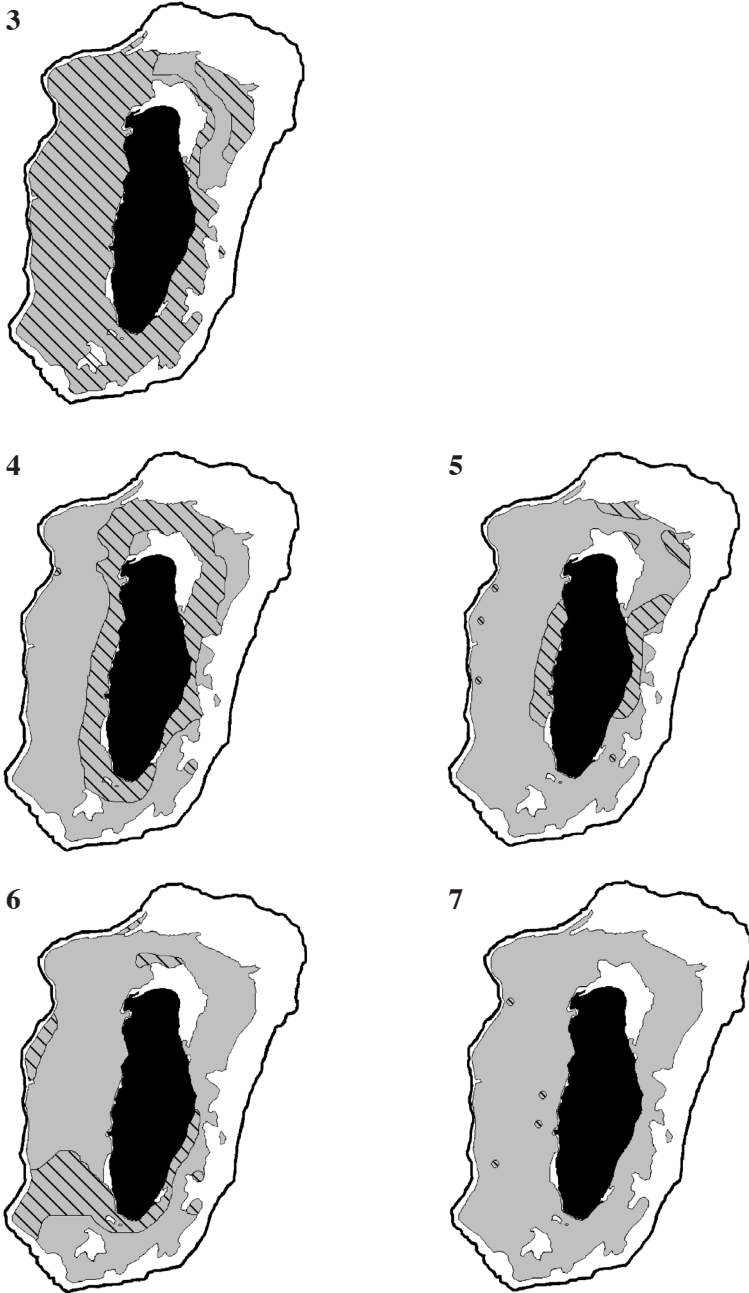
Discussion

Though the invasive ant community on Laysan apparently changed little since the previous comprehensive survey in 1990, the distribution had changed substantially. In 1990, the most widespread ant was *T. bicarinatum*, with *M. pharaonis* restricted to only a small portion of the island near the camp area (Conant and Rowland unpublished). Since that time *M. pharaonis* had displaced *T. bicarinatum* from the bunchgrass habitat and restricted it to the dense vegetation surrounding the lake. *Monomorium pharaonis* had been present on Laysan for twenty years but did not become the dominant species for at least seven years and possibly much longer. What factors led to this shift are unknown but Laysan demonstrates that shifts in dominance amongst invasive ants may occur gradually.

One species of ant may have been extirpated since the last survey of the island. *T. similimum*, possibly the most recently introduced species, was not recorded despite being the second most widespread species during the previous survey in 1990 (Conant and Rowland unpublished). However, it cannot be ruled out that this species was missed if it continues to persist on the island in small numbers.

Five of the eleven ant species recorded on the island have been extirpated in the past 110 years. However, it is possible that the extirpations of *Monomorium destructor*, *Monomorium liliuokalanii*, and *Tapinoma melanocephalum* were greatly influenced by the ecological devastation caused by rabbits considering they were not collected after the loss of the island's vegetation (Table 1). Morrison (1996) found that introduced ants rarely become extirpated once introduced to Polynesian Islands. With only two extirpations since the island was revegetated, Laysan appears to support this trend. This is especially true if we consider that one of the species extirpated was *Pheidole megacephala*. This species has experienced a high level of success in both the main and Northwest Hawaiian Islands, but was recorded in only a single survey on Laysan in 1959 and not seen again despite several additional surveys in the following years (Butler and Usinger 1963). It is possible that this record was from a very recently introduced nonbreeding population at the time of its collection, and the species was never truly established on Laysan.

Though it was possible to rigorously document the invasive ant fauna on Laysan, their impact on the island remains relatively unexplored. Addressing this deficiency should be given the highest of priorities. Though a mass extinction of endemic arthropods likely occurred on the island due to the devastation caused by rabbits (Asquith 1995), Laysan remains an important source of arthropod biodiversity in the archipelago with at least seven endemics and numerous native species surviving (Asquith 1994). Moreover, knowledge of Laysan's



Figures 3–7. Distribution of (3) *M. pharaonis*, (4) *T. bicarinatum*, (5) *M. floricola*, (6) *C. minutior*, and (7) *P. alluaudi* (crosshatched) on Laysan Island, Northwest Hawaiian Islands. Black is the hypersaline lake; grey is vegetation.

native arthropod fauna is deficient taxonomically and research may yield additional endemics (Asquith 1994). The greatest threat to these remaining species is likely invasive ants, as all present species are insectivorous (Gray et al. 1995, Way et al. 1989, Torres 1984, Smith 1965, Sudd 1960). In addition, invasive ants may have indirect impacts through resource competition, facilitative relationships with other alien species, or further disruptions to Laysan's already altered ecosystem through soil excavation, seed predation, etc. (Holway et al. 2002). Having not been thoroughly surveyed for over a decade the current status of many of these species is poorly understood and additional extinctions are possible without further monitoring and research. If invasive ants are found to be negatively affecting the biota of Laysan, options for control and eradication should be explored.

Eradicating invasive ants from large natural areas is a relatively new area of research. Few eradications have been attempted and successful programs have involved relatively small areas (<30 ha) and referred to only one or two species, ignoring other nonnative ant species that may have been present (Causton et al. 2005, Hoffman and O'Connor 2004, Abedrabbo 1994). With an area of 217 ha occupied by six ant species, eradicating ants from Laysan represents an exceptional challenge even when budgetary issues are not considered. The island's large size suggests broadcasting insecticidal bait is the only viable control method. However, broadcasting leaves the bait subject to weather effects that may limit its longevity either through reduced palatability to foraging ants or degradation of the insecticidal agent (Krushelnicky and Reimer 1998) leading to frequent reapplications. In addition, a bait or mixture of baits that is attractive to all ant species is required to prevent unaffected species from expanding their range into areas vacated by affected species. This may prove difficult considering that the widespread *M. pharaonis* may rapidly change its food preference and baits are unlikely to remain attractive over long periods of time (Edwards and Abraham 1990). In addition, some of the most commonly used ant baits such as Amdro, Maxforce, and Advance have already been found to be unattractive to *M. pharaonis* on Laysan Island (McClelland and Jones unpublished data). Finally, the presence of endemic arthropods as well as the endemic and endangered Laysan Duck (*Anous laysanensis*) and Laysan Finch (*Telespiza cantans*) requires non-target effects to be thoroughly explored before an eradication program could be initiated and may limit options.

Though Laysan presents a number of challenges, there are a number of factors that may aid a successful eradication program. All ant species present on the island, with the exception of the uncommon *H. punctatissima*, spread by budding (Heinze et al. 2006, Trontti 2006, Astruc et al. 2001, Smallwood 1982). This suggests that if an effective control method can be found, ant-free areas can be established, maintained, and expanded. In addition, this study found no new species of invasive ant suggesting the quarantine measures established for the island are adequate. In combination with a year-round UFWS presence to monitor for new introductions, the risk of reinvasion is low.

Perhaps a threat to biodiversity on Laysan greater than the current invasive ant community is the introduction of additional and more aggressive ant species. Thus far Laysan has avoided the introduction of the most damaging of invasive ants including *Anoplolepis gracilipes*, *Linepithema humile*, *Wasmannia auropunctata*, *Solenopsis geminata*, and *P. megacephala* (Holway et al. 2002). However, all of these species are present in Hawaii (Krushelnicky et al. 2005) with the latter two also present in the Northwest Hawaiian Islands (Nishida and Beardsley 2002). It is imperative that quarantine measures are maintained and the island continued to be monitored for additional introductions. Without quarantine measures, the introduction of additional invasive ants to the Northwest Hawaiian Islands is certain to occur and is a substantial threat to native fauna and flora. This is perhaps best demonstrated by Tern Island, an unquarantined island 540 km southeast of Laysan that experienced 2 ant introductions between 2001 and 2005 (McClelland and Jones unpublished data).

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Literature Cited

- Abedrabbo, S.** 1994. Control of the little fire ant *Wasmannia auropunctata*, on Santa Fe Island in the Galápagos Islands pp. 219–227. In D.F. Williams (ed.), *Exotic ants: biology, impact, and control of introduced species*. Westview Press, Boulder, CO, USA.
- Asquith, A.** 1995. Alien species and the extinction crisis of Hawaii's invertebrates. *Endangered Species Update* 12: 6–12.
- Asquith, A.** 1994. The arthropod fauna of Laysan Island. U.S. Fish and Wildlife Service, Honolulu, HI, USA.
- Astruc, C., C. Malosse, and C. Errard.** 2001. Lack of intraspecific aggression in the ant *Tetramorium bicarinatum*: a chemical hypothesis. *Journal of Chemical Ecology* 27: 1229–1248.
- Bach, C.E.** 1991. Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). *Oecologia* 87: 233–239.
- Bryan, E.J. Jr.** and collaborators. 1926. Insects of Hawaii, Johnston Island, and Wake Island. *Bishop Museum Bulletin* 31: 3–16.
- Butler, G.D.** 1961. Insects and other arthropods from Laysan Island. *Proceedings of the Hawaiian Entomological Society* 17: 379–387.
- Butler, G.D., and R.L. Usinger.** 1963. Insects and other invertebrates from Laysan Island. *Atoll Research Bulletin* 98:1–30.
- Causton, C.E., C.R. Sevilla, and S.D. Porter.** 2005. Eradication of the Little Fire Ant, *Wasmannia auropunctata*, from Marchena Island, Galapagos: on the edge of success? *Florida Entomologist* 88: 159–168.
- Delabie, J.H.C., and F. Blard.** 2002. The Tramp Ant *Hypoponera punctatissima* (Roger) (Hymenoptera: Formicidae: Ponerinae): New Records from the Southern Hemisphere. *Neotropical Entomology* 31: 149–151.
- Edwards, J.P., and L. Abraham.** 1990. Changes in food selection by workers of the Pharaoh's ant, *Monomorium pharaonis*. *Medical and Veterinary Entomology* 4: 205–211.
- Ely, C.A., and R.B. Clapp.** 1973. The natural history of Laysan Island, Northwest Hawaiian Islands. *Atoll Research Bulletin* No. 171. Smithsonian Institution, Washington, DC, USA.
- Emery, C.** 1899. Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–97), Formiciden. *Zoologisches Jahrbuch Abteilung für Systematik* 12: 438–440.
- Fullaway, D.T.** 1914. A list of Laysan Island insects. *Proceedings of the Hawaiian Entomological Society* 3:20–22.
- Gerlach, J.** 2004. Impact of the invasive crazy ant *Anoplolepis gracilipes* on Bird Island, Seychelles. *Journal of Insect Conservation* 8: 15–25.
- Gray, K.J., C. Porter, P.M. Hawkey, S.G. Compton and J.P. Edwards.** 1995. Roger's ant: a new pest in hospitals. *British Medical Journal* 311: 129.
- Haskins C.P., and E.F. Haskins.** 1965. *Pheidole megacephala* and *Iridomyrmex humilis*. Bermuda-equilibrium or slow replacement? *Ecology* 46: 736–740.
- Heinze, J., S. Cremer, N. Eckl, and A. Schrempf.** 2006. Stealthy invaders: the biology of *Cardiocondyla* tramp ants. *Insectes Sociaux* 53: 1–7.
- Hoffman, B.D., and S. O'Connor.** 2004. Eradication of two exotic ants from Kakadu National Park. *Ecological Management and Restoration* 5: 98–105.
- Holway, D.A., L. Lach, V.A. Suarez, N.D. Tsutsui, and T.J. Case.** 2002. The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics* 33: 181–233.
- Hosmer, D.W., and S. Lemeshow.** 1989. *Applied logistic regression*. Wiley, NY, USA.
- Illingworth, J.F.** 1917. Economic aspects of our predaceous ant (*Pheidole megacephala*). *Proceedings*

- of the Hawaiian Entomological Society 3:349–368.
- Krushelnicky, P.D., and N.J. Reimer.** 1998. Efficacy of Maxforce bait for control of the Argentine ant (Hymenoptera: Formicidae) in Haleakala National Park, Maui, Hawaii. *Environmental Entomology* 27: 1473–1481.
- Krushelnicky, P.D., L.L. Loope, and N.J. Reimer.** 2005. The ecology, policy, and management of ants in Hawaii. *Proceedings of the Hawaiian Entomological Society* 37: 1–25.
- Lach, L.** 2007. A mutualism with a native membracid facilitates pollinator displacement by argentine ants. *Ecology* 88: 1994–2004.
- Lamoureux, C.H.** 1963. The flora and vegetation of Laysan Island. *Atoll Research Bulletin* 97.
- Le Breton, J.L., H. Jourdan, J. Chazeau, J. Orivel, and A. Dejean.** 2005. Niche opportunity and ant invasion: the case of *Wasmannia auropunctata* in a New Caledonian rain forest. *Journal of Tropical Ecology* 21: 93–98.
- Lubin, Y.D.** 1984. Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant, *Wasmannia auropunctata*. *Biological Journal of the Linnean Society* 21: 229 – 242.
- Minitab Inc.** 2000. Minitab user's guide 1 and 2. Minitab Inc., State College, PA, USA.
- Morrison, L.W.** 1996. Community organization in a recently assembled fauna: the case of Polynesian ants. *Oecologia* 107:243–256.
- Moulton, D.W., and M.W. Weller.** 1984. Biology and conservation of the Laysan Duck (*Anas lay-sanensis*). *Condor* 86: 105–117.
- Ness, J.H., and J.L. Bronstein.** 2004. The effects of invasive ants on prospective ant mutualists. *Biological Invasions* 6: 445–461.
- Newman, A.L.** 1988. Mapping and monitoring vegetation change on Laysan Island. M.A. thesis, Department of Geography, University of Hawaii Manoa, Honolulu, HI, USA.
- Nishida, G.M.** 2001. NOWRAMP 2000 Terrestrial Arthropod Report. U.S. Fish & Wildlife Service, Honolulu, HI, USA.
- Nishida, G.M., and J.W. Beardsley.** 2002. A review of the insects and related arthropods of Midway Atoll. *Bishop Museum Occasional Papers* 68: 25–69.
- Paulay, G.** 1994. Biodiversity on oceanic islands: its origin and extinction. *American Zoologist* 34:143–144.
- Philpott, S.M., R. Greenberg, and P. Bichier.** 2005. The influence of ants on the foraging behavior of birds in an agroforest. *Biotropica* 37: 468–471.
- Smallwood, J.** 1982. Nest relocations in ants. *Insectes Sociaux* 29: 138–147.
- Smith, M.R.** 1965. House-infesting ants of the eastern United States. Washington, U.S. Dept Agriculture Technical Bulletin No.1326.
- Smith, M.R.** 1958. A contribution to the taxonomy, distribution and biology of the vagrant ant, *Plagiolepis alluaudi* Emery (Hymenoptera, Formicidae). *Journal of the New York Entomological Society* 65: 195–198.
- Sudd, J.H.** 1960. *The foraging method of Pharaoh's ant, Monomorium pharaonis (L.)* *Animal Behaviour* 8: 67–75.
- Torres, J.A.** 1984. Niches and coexistence of ant communities in Puerto Rico: repeated patterns. *Biotropica* 16: 284–295.
- Trontii, K.** 2006. Population structure and evolution in the ant *Plagiolepis pygmaea* and its two social parasites *Plagiolepis xene* and *Plagiolepis grassei*. Academic dissertation, Faculty of Biosciences of the University of Helsinki, Finland.
- Tsutsui, N.D., and A.V. Suarez.** 2003. The colony structure and population biology of invasive ants. *Conservation Biology* 17:48–58.
- Way, M.J., M.E. Cammell, B. Bolton, and P. Kanagaratnam.** 1989. Ants (Hymenoptera: Formicidae) as egg predators of coconut pests, especially in relation to biological control of the coconut caterpillar, *Opisina arenosella* Walker (Lepidoptera: Xyloryctidae), in Sri Lanka. *Bulletin of Entomological Research* 79: 219–233.
- Way, M.J., Z. Islam, K.L. Heong, and R.C. Joshi.** 1998. Ants in tropical irrigated rice: distribution and abundance, especially of *Solenopsis geminata* (Hymenoptera: Formicidae). *Bulletin of Entomological Research* 88: 467–476.
- Wilson, E.O., and R.W. Taylor.** 1967. The ants of Polynesia (Hymenoptera: Formicidae). *Pacific Insects Monograph* 14: 1–109.